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Research Article

History of the introduction of a species resembling the benthic foraminifera *Nonionella stella* in the Oslofjord (Norway): morphological, molecular and paleo-ecological evidences

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Abstract

Specimens resembling the benthic foraminifera *Nonionella stella* (Cushman and Moyer, 1930), a morphospecies originally described from the San Pedro Basin, California, USA, were observed for the first time in the Oslofjord (Norway) in 2012. This study investigates the Oslofjord *Nonionella* population in order to confirm its non-indigenous species (NIS) status and assess its introduction time. Morphological characterisation based on SEM imaging complemented by molecular identification using small subunit (SSU) rDNA sequencing and assessment of the recent past record (sediment core), were performed on material collected in the Oslofjord in 2016. Examination of the dead fauna showed that specimens resembling *N. stella* only appeared recently in the Oslofjord, confirming the NIS status of this population. Moreover, DNA results indicate that the Oslofjord specimens differ genetically from *N. stella* sampled in the Santa Barbara Basin (California USA). Hence, we propose to use the name *Nonionella* sp. T1 for the specimens sampled in the Oslofjord for the time being. In the southern part of the Skagerrak, specimens morphologically similar to *Nonionella* sp. T1 were reported as NIS in the Gullmar fjord (Sweden) in 2011 and in the Skagerrak in 2015. Molecular data indicate that the two populations from Gullmar- and Oslofjords are identical, based on their SSU rDNA sequences. In addition, analyses of foraminiferal dead assemblages suggest that the population from the Gullmar fjord settled prior to the Oslofjord population, *i.e.* ~ 1985 and about 2010, respectively. This implies that *Nonionella* sp. T1 may have been transported from Sweden to Norway by northward coastal currents.

Key words: non-indigenous species, benthic foraminifera, morphological criteria, molecular identification

Introduction

Introduction of non-indigenous species (NIS) is one of the major threats to biodiversity and ecosystem functioning in coastal waters (Butchart et al. 2010; Pyšek and Richardson 2010). One of the main vectors of NIS

introductions is ballast water (Oliveira 2007). In 2001, maritime shipping carried 90% of the world's 5.1 billion tons of international trade (Kite-Powell 2008) and every day, more than 10,000 species are likely to be transported around the world in the ballast tanks of cargo ships (Carlton 1987; Carlton and Geller 1993). Fortunately, most of those potential invaders do not survive due to unsuitable environmental conditions (Bax et al. 2003). However, some taxa among certain groups (*e.g.* fish, algae, benthic foraminifera and benthic macro-invertebrates) have a high survival potential and may potentially, colonise the "introduction site" (Wonham et al. 2000; Occhipinti-Ambrogi et al. 2010). According to model predictions on the spread of marine species introduced by global shipping, Northern European seas are one of the ecoregions, which are characterised by a high risk of NIS invasions (Seebens et al. 2016). Among the 167 alien species introduced into the North Sea, the majority belongs to large and well-studied taxa, with only three protist species reported (Gollasch et al. 2009). Hence, there is a lack of knowledge on smaller body-sized taxa, especially on meiofauna-sized organisms (Occhipinti-Ambrogi et al. 2010), which include foraminifera. These were found alive in ballast water (Galil and Hülsmann 1997). It has been shown that at least, some foraminifera are easily transported as resting stages (propagules) and can survive unsuitable environmental conditions (Alve and Goldstein 2003, 2010). Once non-indigenous benthic foraminifera have been introduced and colonised a new area, a further dispersion of propagules (with *e.g.* currents) is a way by which foraminifera could extend their distribution from local to regional geographical scales as long as they find a suitable environment. Introduction of non-indigenous benthic foraminifera by means of ballast water has been reported already (*e.g.* McGann et al. 2000; Bouchet et al. 2007). For example, the benthic foraminifera *Trochammina hadai* Uchio, 1962 was introduced in the San Francisco Bay in 1983 by ballast water and today, the species accounts for more than 50% of the foraminiferal assemblage in the bay while it contributed only 1.5% when it first appeared (McGann et al. 2000, 2012).

To date only a few studies have reported NIS foraminifera (McGann and Sloan 1996; Hayward 1997; Hayward et al. 1999; Tapiero 2002; Oflaz 2006; Bouchet et al. 2007; Grenfell et al. 2007; Hyams-Kaphzan et al. 2008; Langer 2008; Pawlowski and Holzmann 2008; Calvo-Marcilese and Langer 2010; Schweizer et al. 2011; Almogi-Labin and Hyams-Kaphzan 2012; Milker and Schmiedl 2012; Merkado et al. 2013, 2015; Polovodova Asteman and Schönfeld 2015; Langer and Mouanga 2016). Half of these studies concern the Mediterranean Sea, particularly its Eastern part (see Zenetos et al. 2010, 2012 for more details). Thorough investigations of sediment core records are needed to determine the introduction period of a species, assuming this NIS has a high preservation potential once dead. In contrast to many macroinvertebrates, foraminiferal tests are preserved in the sediment after death, and can be recorded in sediment cores, thus

providing information on their introduction time. However, among the worldwide-recorded foraminiferal NIS species, only a few studies performed such an assessment (McGann et al. 2012; Polovodova Asteman and Schönfeld 2015; Langer and Mouanga 2016). Furthermore, over the last decades, molecular methods have become a powerful and increasingly informative tool in NIS investigations, providing integral information on a species' source, vector, spread, and introduction time (Sakai et al. 2001; Voisin et al. 2005). To complement morphological analyses by Scanning Electron Microscope (SEM) imaging, a molecular identification with rDNA sequences helps confirm taxonomic denomination and understanding a species' source using phylogenetic analyses (Pawlowski 2000; Hayward et al. 2004; Pawlowski and Holzmann 2008; Schweizer et al. 2011).

The benthic foraminifera *Nonionella stella* (Cushman and Moyer, 1930) was originally described from the Northeast Pacific Ocean and its taxonomic history is complicated. Indeed, Rhumbler (1949) used the Californian fossil species *Nonionella miocenica* (Cushman, 1926) to define the genus *Nonionella.* A new variant of *N. miocenica*, *Nonionella miocenica* variety *stella* was then observed and described in the San Pedro Basin, California (Cushman and Moyer 1930). This morphotype was raised to the species level by Lankford and Phleger (1973) under the name *Nonionella stella*. It is described as an ubiquitous morphospecies displaying a large geographical presence in different ecosystems such as oxygen minimum zones of the eastern Pacific (Ingle et al. 1980; Culver and Buzas 1987; Kato 1992; Bernhard and Bowser 1999; Murray 2006), anoxic basins off California (Bernhard et al. 1997) and Tunisia (Martins et al. 2016), well-oxygenated ecosystems in British Columbia (Patterson et al. 2000) and in upwelling zones off Namibia (Leiter and Altenbach 2010) (see Polovodova Asteman and Schönfeld 2015 for more details). Specimens first attributed to the morphospecies *N. stella* were observed alive in the surface sediment of the Gullmar fjord in 2011, whereas a sediment core-based study showed that this taxon was introduced to the area for the first time in 1985 (Polovodova Asteman and Schönfeld 2015). In the adjacent Skagerrak and Kattegat regions (*e.g.* Øresund strait, Dynekilen fjord, Sannäs fjord) the morphospecies was recorded among living (stained) fauna for the first time in 2013 (see Polovodova Asteman and Schönfeld 2015; Charrieau et al. 2018 for more details). In addition, benthic foraminifera resembling *N. stella* were observed for the first time in 2012 in the Oslofjord (Norway) (Alve and Hess, *pers. comm.*). Morphological differences, between individuals from California (Bernhard and Bowser 1999) and the Gullmar fjord (Polovodova Asteman and Schönfeld 2015) suggest that these populations may belong to different species sharing a roughly similar morphology attributed to the morphospecies *N. stella* (see discussion below). Hence, molecular analyses and a detailed morphological analysis based on SEM images of sequenced specimens are needed to confirm or refute the taxonomical identification

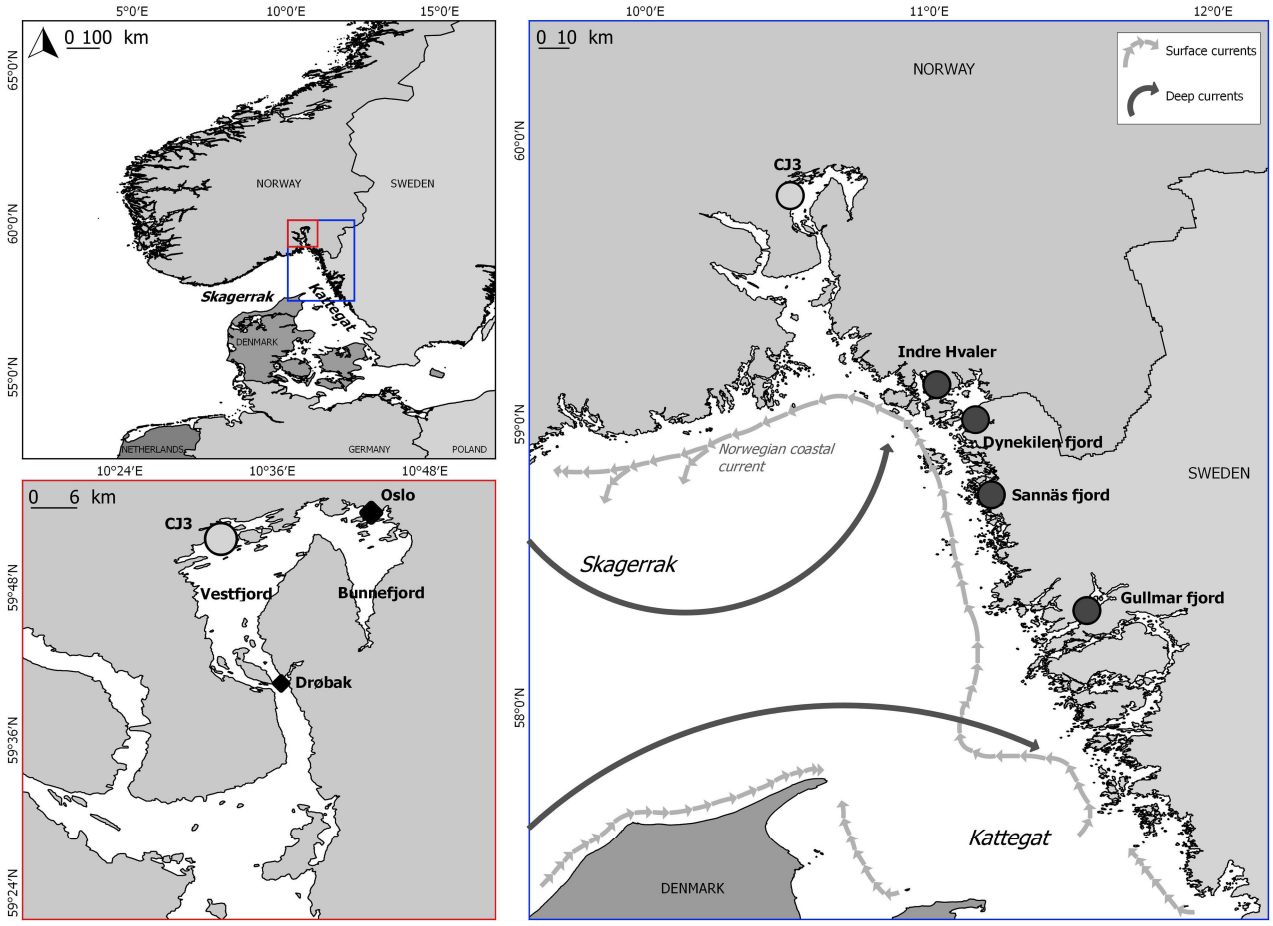

Figure 1. Geographical location of station Cj3-2016 in the Oslofjord, Norway, and the four other sites used for comparison (*i.e.* Gullmar fjord, Sannäs fjord, Dynekilen fjord and Indre Hvaler). Black and dotted arrows respectively represent deep and surface currents (data from National Geospatial Intelligence Agency).

of the individuals from the Oslofjord, which have been included in the morphospecies *N. stella* in previous studies.

The objectives of this study are fourfold: (*i*) to identify the new *Nonionella* species in the Oslofjord using molecular tools, *(ii)* to combine molecular and morphological data to characterise it morphologically, (*iii*) to assess the occurrence of this taxon over the last decades in the Oslofjord using dead assemblages, which will help to validate its NIS status, and (*iv*) to trace back the species origin using molecular tools.

Materials and methods

Sampling strategy

The Oslofjord sediment samples were collected on the 22nd of August 2016 at station Cj3-2016 located in a semi-enclosed basin of the Vestfjord (59°50.683′N; 10°30.603′E, 58 m water depth, Figure 1) using the R/V Trygve Braarud (University of Oslo, Norway). The station was sampled by previous studies (Dolven et al. 2013) and was chosen because its environmental features are well known and it is located only a few km away from the site where foraminifera resembling *Nonionella stella* were observed in 2012.

Surface sediments (0–2 cm) were sampled using a 1.0 m^2 van Veen grab for the isolation and analysis of living *Nonionella* specimens morphologically resembling *N. stella* (further referred to as *Nonionella* sp.). Samples were stored at ambient temperature (7 °C) with *in situ* seawater in transparent plastic 1000 ml containers in dark cold-incubators until living individuals were picked for morphological and molecular analyses. In addition, six sediment cores (∅ 8 cm) were collected using a "Gemini twin barrel corer" (a modified Niemistö corer, Niemistö 1974). The least disturbed core was selected for studying the dead foraminiferal faunas and radiometric dating. After the 17 cm core was collected, it was divided into 1 cm thick slices (*i.e.* 0–1 cm, 1–2 cm, etc.) and the samples were stored in a freezer.

In order to identify the regional source of the *Nonionella* species, this study uses previously published work on the Skagerrak-Kattegat adjacent fjords *e.g.* Gullmar, Sannäs and Dynekilen fjords (Polovodova Asteman and Schönfeld 2015 and references therein). However, some aspects of that study were never published and are presented in this paper. Molecular analyses were used to compare the specimens resembling *Nonionella* sp. in the Oslofjord to those from the Gullmar fjord (also presented herein). Hence, surface sediment samples for living foraminifera and molecular analyses were collected in September 2011 at the G113 station (58°17.570′N; 11°23.060′E, 116 m water depth) (see Polovodova Asteman and Schönfeld 2015 and reference therein for more details).

Dating of sediments

Sediment slices from the Oslofjord core were freeze-dried and the water content was determined prior to dating. These samples were sent to the Gamma Dating Center (Denmark) where they were analysed for ^{210}Pb, ^{226}Ra and ^{137}Cs activity gamma spectrometry carried out on a Canberra ultralow-background Ge-detector. The constant rate of supply (CRS) modelling was applied to the profile using a method modified from Appleby (2001).

Benthic foraminifera

Preparation of living *Nonionella* sp. for morphological and molecular analyses

The surface sediment samples were washed through a 125-µm sieve (Oslofjord samples) and a 63-µm sieve (Gullmar fjord samples) with *in situ* seawater. Sixty-four (Oslofjord) and twenty-one (Gullmar fjord) specimens of living *Nonionella* were selected using a stereomicroscope. During picking, the sediment was covered with seawater and was kept on ice in order to keep the specimens alive. Living foraminifera were distinguished from dead ones by a greenish colour of protoplasm, and their ability to either stick to the bottom of plastic containers or to move when left over night

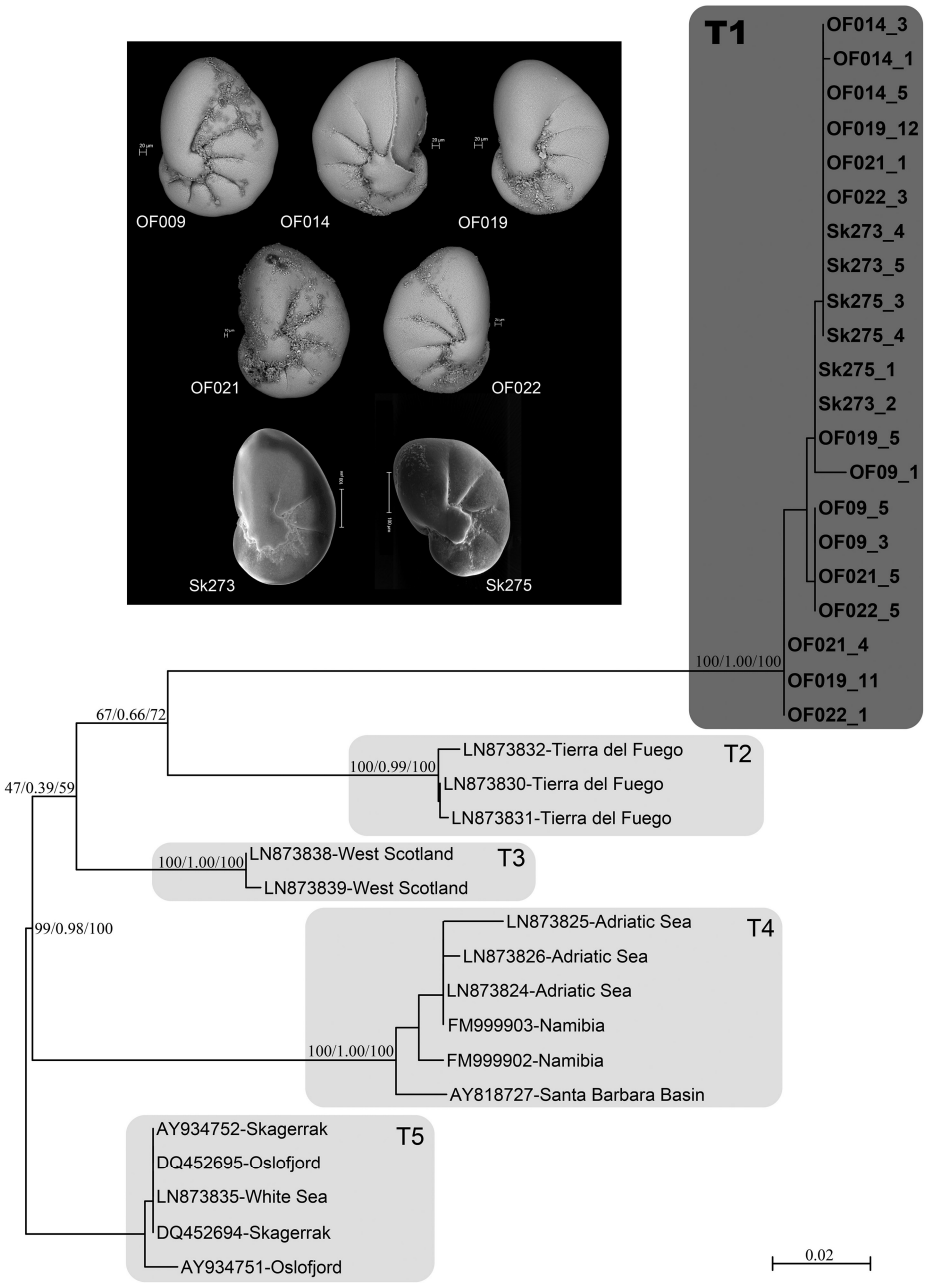

Figure 2. Molecular phylogeny of sequenced nonionids based on partial SSU rDNA sequences inferred using the ML method with the GTR model. The tree is rooted on the phylotype T5 and support values for BioNJ, ML aLRT and ML BS are indicated at the main nodes.

(Pawlowski 2000; Schweizer et al. 2005). Live specimens were cleaned in filtered seawater with a brush to remove remaining sediment. Specimens were then transferred to Eppendorf tubes and were dried at room temperature, ready for SEM imaging and molecular analyses.

SEM imaging, morphological and molecular analyses

All *Nonionella* individuals selected for genetic characterisation were SEM imaged prior to molecular analyses (Figure 2). The dried specimens were placed on a stub and the Gullmar fjord specimens were gold coated and imaged using an SEM (Philips XL30CP) at the Grant Institute (University

of Edinburgh), whereas the Oslofjord specimens were examined without coating with an environmental SEM (EVO LS10, Zeiss) at the Laboratory SCIAM (University of Angers).

The specimens were then individually extracted for DNA in Deoxycholate (DOC) buffer (Pawlowski 2000). For the DNA amplification by Polymerase Chain Reaction (PCR), a fragment situated at the 3' end of the small subunit (SSU) rDNA was selected because this region is the barcode for foraminifera (Pawlowski and Holzmann 2014). The primer pairs were s14F3 and J2 for the primary PCR and s14F1 and N6 for the secondary (nested) PCR (Pawlowski 2000; Darling et al. 2016). The PCR conditions were 2 min at 94 °C followed by 40 cycles of 94 °C for 30 s, 50 °C for 30 s, 72 °C for 2 min and ending with 72 °C for 10 min. For the secondary amplification, parameters remained unchanged except for the annealing temperature (52 °C) and cycle number (30). Positive PCR reactions resulted in a fragment of about 500 nucleotides (nt). Most of the PCR products were sequenced directly as described in Schweizer et al. (2011). Several specimens were selected for cloning to document the intra-individual variation (Pawlowski 2000) within the studied population. They were amplified using the primer pairs s14F3-sB (Pawlowski 2000) and s14F1-J2 to obtain a fragment of about 1000 nt, purified using the High Pure PCR Purification Kit (Roche Diagnostics) and ligated into the P-GEMt-easy vector (Promega). Transformations were carried out in JM109 (Promega) competent cells according to the manufacturer' protocol and the inserts were subsequently sequenced. Positive samples (direct amplifications and clones) were sequenced with the Sanger method at the GenePool (University of Edinburgh), the Plateforme Génomique (University of Nantes) or GATC Biotech (Konstanz).

New DNA sequences (Table 1) were deposited in GenBank (accession numbers MH016669–MH016736). All sequences obtained were edited, automatically aligned together with available sequences of nonionids from GenBank with MUSCLE (Edgar 2004) implemented in SeaView 4 (Gouy et al. 2010) and then corrected manually to obtain an alignment of 1203 sites. Twenty-one cloned sequences belonging to seven individuals were chosen for phylogenetic analyses, together with sequences of nonionids from GenBank (Figure 2, Table 2). The regions that were impossible to align properly were removed to obtain a final alignment of 674 sites (the number of sites calculated with Seaview). Maximum likelihood (ML) analyses were performed by PhyML (Guindon and Gascuel 2003) implemented in Seaview under the GTR (General Time Reversible) evolutionary model (Tavaré 1986). The statistical support was calculated either with non-parametric bootstrapping (100 replicates) or the aLRT (approximate Likelihood Ratio Test) branch support (Anisimova and Gascuel 2006). In addition, BioNJ (Neighbor Joining) phylogenetic trees (Gascuel 1997) were inferred with Seaview under the K2P (Kimura's two parameter) evolution model (Kimura 1980) with non-parametric bootstrapping (1 000 replicates).

Table 1. *Nonionella* sp. T1 samples sequenced for this study with their DNA isolates, sampling location, primers used for amplification, sequencing (direct or cloning) and GenBank accession numbers (sequences < 200 nt are not accepted).

DNA isolate	Sampling location	Sequenced fragment (primers)	Sequencing	Accession numbers
OF02	Oslofjord	s14-N6	Direct	MH016669
OF04	Oslofjord	s14-N6	Direct	MH016670
OF05	Oslofjord	s14-N6	Direct	MH016671
OF08	Oslofjord	s14-N6	Direct	MH016672
OF09	Oslofjord	s14-J2	3 clones	MH016673–MH016675
OF011	Oslofjord	s14-N6	Direct	< 200 nt
OF012	Oslofjord	s14-N6	Direct	MH016676
OF013	Oslofjord	s14-N6	Direct	< 200 nt
OF014	Oslofjord	s14-J2	4 clones	MH016677–MH016680
OF015	Oslofjord	s14-N6	Direct	MH016681
OF016	Oslofjord	s14-N6	Direct	MH016682
OF019	Oslofjord	s14-J2	20 clones	MH016683–MH016702
OF021	Oslofjord	s14-J2	5 clones	MH016703–MH016707
OF022	Oslofjord	s14-J2	5 clones	MH016708–MH016712
OF026	Oslofjord	s14-N6	Direct	MH016713
OF031	Oslofjord	s14-N6	Direct	< 200 nt
OF034	Oslofjord	s14-N6	Direct	< 200 nt
OF036	Oslofjord	s14-N6	Direct	MH016714
OF049	Oslofjord	s14-N6	Direct	MH016715
OF052	Oslofjord	s14-N6	Direct	MH016716
OF055	Oslofjord	s14-N6	Direct	< 200 nt
OF062	Oslofjord	s14-N6	Direct	MH016717
Sk256	Gullmar fjord	s14-N6	Direct	MH016718
Sk257	Gullmar fjord	s14-N6	Direct	MH016719
Sk260	Gullmar fjord	s14-N6	Direct	MH016720
Sk265	Gullmar fjord	s14-N6	Direct	MH016721
Sk269	Gullmar fjord	s14-N6	Direct	MH016722
Sk272	Gullmar fjord	s14-N6	Direct	MH016723
Sk273	Gullmar fjord	s14-N6 s14-J2	Direct 4 clones	MH016724 MH016725–MH016728
Sk274	Gullmar fjord	s14-N6	Direct	MH016729
Sk275	Gullmar fjord	s14-N6 s14-J2	Direct 5 clones	MH016730 MH016731–MH016735

Table 2. SSU rDNA sequences of nonionids taken from GenBank and used for phylogenetic analyses.

Accession number	Morphological Identification	Sampling location	Reference
AY934751	*Nonionellina labradorica*	Oslofjord	Schweizer et al. 2005
AY934752	*Nonionellina labradorica*	Skagerrak	Schweizer et al. 2005
DQ452694	*Nonionellina labradorica*	Skagerrak	Schweizer 2006
DQ452695	*Nonionellina labradorica*	Oslofjord	Schweizer 2006
LN873835	*Nonionellina labradorica*	White Sea	Holzmann and Pawlowski 2017
LN873830	*Nonionella* sp.	Tierra del Fuego	Holzmann and Pawlowski 2017
LN873831	*Nonionella* sp.	Tierra del Fuego	Holzmann and Pawlowski 2017
LN873832	*Nonionella* sp.	Tierra del Fuego	Holzmann and Pawlowski 2017
LN873838	*Nonionoides turgidus*	West Scotland	Holzmann and Pawlowski 2017
LN873839	*Nonionoides turgidus*	West Scotland	Holzmann and Pawlowski 2017
FM999902	*Nonion* sp.	Namibia	Grimm et al., *unpublished*
FM999903	*Nonion* sp.	Namibia	Grimm et al., *unpublished*
LN873824	*Nonion* sp.	Adriatic Sea	Holzmann and Pawlowski 2017
LN873825	*Nonion* sp.	Adriatic Sea	Holzmann and Pawlowski 2017
LN873826	*Nonion* sp.	Adriatic Sea	Holzmann and Pawlowski 2017
AY818727	*Nonionella stella*	California, USA	Bernhard et al. 2006

Preparation and analysis of dead foraminifera

The dried Oslofjord sediment core samples were gently homogenised, and 6 g of dry sediment from each sample was weighed, washed through a 125-µm sieve and examined under a stereomicroscope. One thousand specimens (tests) per sample were picked, mounted on microslides and identified at the morphospecies level. Shallow water taxa, such as *Cibicidoides lobatulus, Elphidium* sp. (approximatively 10% per sample), which may have been transported to the site by currents, were subtracted from the dataset and were not included in the calculations. Relative and absolute abundance of dominant morphospecies (*e.g. Stainforthia fusiformis, Nonionellina labradorica*) including *Nonionella* sp. were calculated for each sample.

Results

Molecular identification and molecular phylogeny of Nonionella *sp. from the Oslo- and the Gullmar fjords*

Of the 85 imaged and dried specimens of *Nonionella* sp. from the Oslo- and the Gullmar fjords (Supplementary material Figures S1, S2, S3, S4), 32 were successfully sequenced for partial SSU rDNA analysis and a total of 73 sequences were obtained either by direct sequencing or after cloning (Table 1, Figures S2, S3). These sequences were aligned with other nonionid sequences retrieved from GenBank for a comparative analysis (Table 2). The two methods (BioNJ and ML) used to build the phylogenetic trees gave the same topology and equally supported branch nodes (Figure 2). Five clades, named T1–T5, were retrieved in these analyses with a very high statistical support and long branches (T1, T3 and T4: 100/1.00/100; T2: 100/0.99/100; T5: 99/0.98/100). The trees were rooted on the phylotype T5, as analyses with a wider dataset (data not shown) placed this clade at the root of the group studied here. The statistical support for grouping the phylotypes together is medium (67/0.66/72 for the group T1+T2) to low (47/0.39/59 for the group T1+T2+T3), which is partially due to the low number of phylogenetically informative sites (674) available for the analyses.

Most of the variations observed in the sequences are concentrated in three specific regions of the partial SSU fragment. The intraspecific variability within phylotypes can be separated into three categories: low values (T3: 0.9%, T5: 0.4%), medium values (T1: 2.3%, T2: 1.7%) and high values (T4: 4.3%). All these values can be considered as intra-specific ones (Weber and Pawlowski 2014). The variability of 2.3% observed in the phylotype T1 is even intra-individual as clones of the individual OF022 vary with this value. However, the higher heterogeneity observed in T4 (variation of 4.3%) could be indicative of inter-specific variation, which may eventually lead to a subsequent splitting of this phylotype, when further evidence becomes available. The phylogenetic tree indicates that

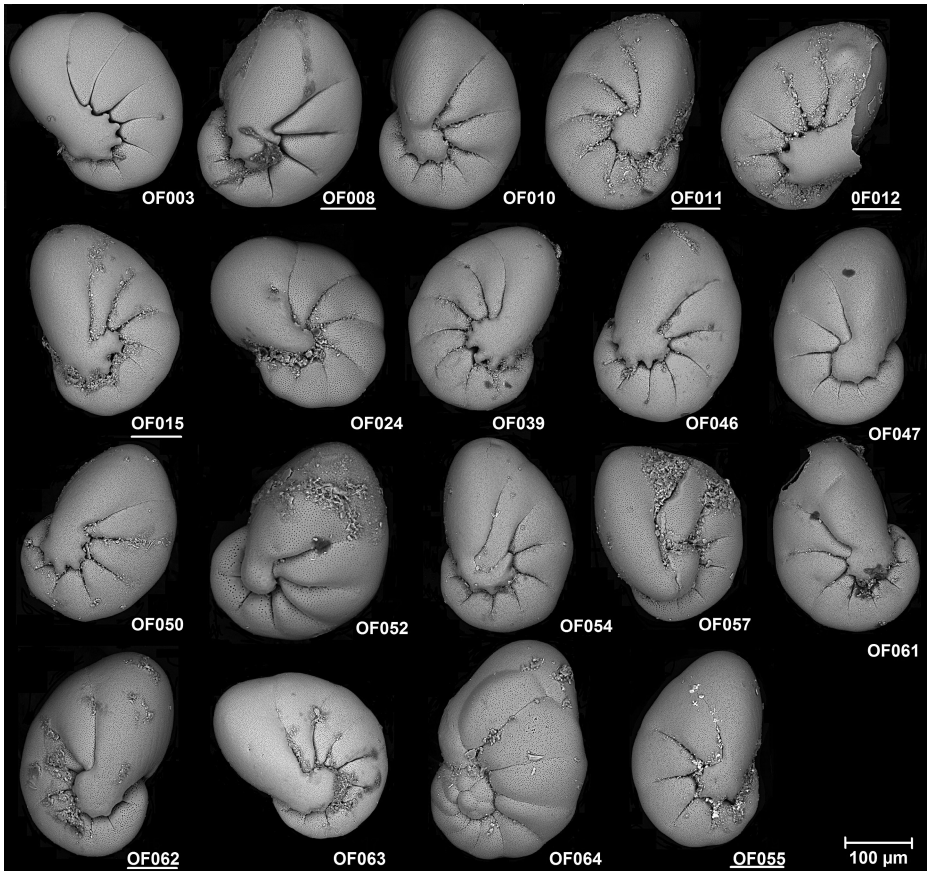

Figure 3. Scanning Electronic Microscope (SEM) images of *Nonionella* sp. T1 (underlined specimen numbers were sequenced, see Table 1) from the Oslofjord station Cj3-2016: 1–17, 19, ventral view; 18, spiral view. Scale bars = 100 µm.

only specimens from the Oslo- and Gullmar fjords fall within phylotype T1 and that they are not found in any other cluster. Therefore, the specimens previously morphologically identified as *N. stella, N.* aff. *stella* or *Nonionella* resembling *stella* in these regions can be classified as phylotype T1.

Morphological description of Nonionella *sp. from the Oslo- and the Gullmar fjords based on sequenced specimens*

A morphological description of the test based on SEM images from the 32 sequenced individuals belonging to phylotype T1 (Figures S2, S3) reveals a trochospiral chamber arrangement, an elongated rounded periphery and a chamber shape with asymmetry between dorsal and ventral sides. The chamber height grows regularly with the last chambers higher than the first ones. The dorsal side is involute and the earlier chambers' axial zone is covered by a lobate extension of the final chamber with more or less developed finger-like processes over the sutures (Figure 3). Note that, the extension morphology can go from round and drop-shaped (*e.g.* Figure 3 individuals n°OF047, OF052 and OF062) to well-developed finger-like processes (*e.g.* Figure 3 individuals n° OF003, OF010 and OF050) with all the intermediate stages. The ventral side is evolute with the older whorls visible. Sutures are slightly depressed over the periphery but deeply depressed

Table 3. Radiometric dates and sediment accumulation rates for the dated sediment core Cj3-2016 in the Oslofjord, Norway.

Depth (cm)	Age (years)	Acc rate ($kg.m^{-2}.y^{-1}$)
0.0	2016	
0.5	2015	1.23
1.5	2012	1.07
2.5	2008	0.90
3.5	2004	1.02
4.5	2001	1.08
5.5	1996	0.84
6.5	1990	0.83
7.5	1985	0.83
8.5	1978	0.70
9.5	1969	0.55
10.5	1957	0.41
11.5	1945	0.38
12.5	1925	0.26
13.5	1893	0.17

close to the axis centre, which is inflated on the ventral side and is hidden by the lobate extension on the dorsal side.

Downcore records of Nonionella *sp. in the Oslofjord*

Chronology

Radiometric dating resulted in a reliable chronology for 0 to 12 cm of the Oslofjord sediment core corresponding to a time scale from 1945 to the present. The ^{137}Cs profile indicates that the 12–14 cm sediment core sample and the rest of the downcore samples (*i.e.* 14–17cm) are affected by mixing (Figure S5). The sediment accumulation rate ranges between 0.17 and 1.23 $kg.m^{-2}.year^{-1}$ and the site has experienced a marked increase in sedimentation rate since about 1980 (Table 3).

Foraminiferal assemblages

In order to determine approximately the period when *Nonionella* sp. first appeared in Vestfjorden, inner Oslofjord (Cj3-2016) and considering the ^{137}Cs chronology is only reliable down to 12 cm depth, only foraminiferal test from the first twelve samples were picked. More than 1,000 specimens were picked from each core sample (Figure 4). Results suggest that this morphospecies appeared for the first time at a depth of 7–8 cm (1 specimen), corresponding to ~ 1985. No individuals were recorded at 6–7 cm (~ 1990) and only one specimen was found at a depth of 5–6 cm (~ 1996). The morphospecies is present in higher abundances between 2008 and 2016 (surface samples *e.g.* 0–1, 1–2, 2–3 cm) and particularly, at 1–2 cm with sixty greenish individuals picked corresponding to 33 *Nonionella* sp. ind./g sediment (Figure 4).

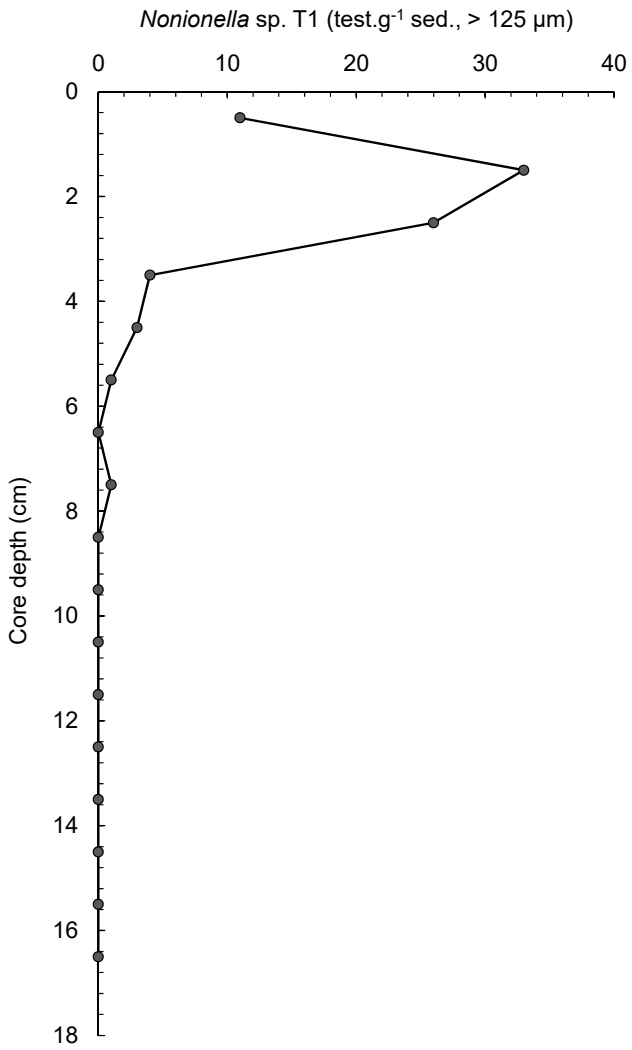

Figure 4. Downcore abundance of *Nonionella* sp. T1 (tests.g^{-1} sed., > 125 µm) for core Cj3-2016 in Oslofjord.

Discussion

What name shall we use for the newcomer in the Oslo- and the Gullmar fjords?

Five benthic foraminiferal morphospecies from the family Nonionidae have previously been identified in the Oslofjord (Alve and Nagy 1990; Alve et al. 2009; Dolven et al. 2013; Hess et al. 2014): *Nonionella auricula* Heron-Allen and Earland, 1930, *Nonionella iridea* Heron-Allen and Earland, 1932, *Nonionellina labradorica* Dawson, 1860, *Nonionoides turgidus* Williamson, 1858, and *Pseudononion japonicum* Asano, 1936 (as *Nonion* sp.). Specimens with finger-like processes over the sutures were not observed in the cited studies. Although their morphological characteristics are different, species identification of deformed and young specimens may be difficult. More specifically, *N. iridea* exhibits a lobate extension of the final chamber covering the umbilicus (Heron-Allen and Earland 1932) and it can be discriminated from *Nonionella* sp. (this study) by its smaller, thin-walled, and

Table 4. Morphological descriptions of *Nonionella miocenica* Cushman, 1926, *Nonionella miocenica* var. *stella* Cushman and Moyer, 1930, *Nonionella* sp. T1 and *Nonionoides turgidus* Williamson, 1858.

***Nonionella miocenica* (Cushman, 1926)**
Cushman JA 1926, pl. 13, fig. 4 a-c
"Test subtrochoid, small, periphery broadly rounded, 8–10 chambers in the last-forming coil, distinct, dorsal side not completely involute; the sutures obliquely curved, the last chambers with umbilical end forming a distinct rounded lobe; wall smooth; aperture elongate."
***Nonionella miocenica* var. *stella* (Cushman and Moyer, 1930), named *Nonionella stella* by Lankford and Phleger 1973**
Cushman JA and Moyer DA 1930, pl. 17, fig. 17 a-b-c
"Variety differing from the typical in the stellate character of the inner end of the last-formed chamber on the ventral side which develops short finger-like processes over the previous sutures."
Cushman JA 1939, pl. 9, fig. 10
"The California form has fewer and broader chambers, and the test is more rounded."
***Nonionella* sp. T1**
Polovodova Asteman and Schönfeld 2015, pl. 1, fig. 1–14
"*Nonionella stella* exhibited a hand-shaped, lobate extension of the final chamber covering the umbilicus with clearly developed finger-like processes over the sutures."
***Nonionoides turgidus* (Williamson, 1858)**
Williamson WC 1858, pl. 4, fig. 95–97
"The second convolution is visible; inferiorly the last few segments are largely developed, becoming remarkably ventricose, especially at their umbilical margins, where they are broad and prominent; the ultimate one concealing a considerable part of the shell."
Cushman JA 1939, pl. 9, fig. 2–3
"Test longer than broad, much compressed, irregularly heart-shaped, periphery rounded, the dorsal side slightly involute, ventral side involute; chambers distinct, increasing rapidly in size and length as added, slightly if at all inflated, except on the ventral side, where the last-formed one has an enlarged portion over the umbilical area."
Polovodova Asteman and Schönfeld 2015, pl.1, fig. 16–18
"The extension is straight, often parallel to a previous chamber or rounded and drop-shaped."

semi-transparent test with an iridescent appearance. Furthermore, another morphospecies whose juveniles may be misidentified as *Nonionella* sp. is *N. turgidus,* which does not have finger-like processes over the sutures and has a more elongated test shape than *Nonionella* sp. (Table 4). In most studies, the taxonomy of benthic foraminifera is still mainly based on morphological criteria. However, cases such as cryptic species (different biological species with identical morphologies), morphological convergence (unrelated species sharing an analogous character) or ecophenotypy (same species looking different under different ecological conditions) are usually impossible to detect using morphology alone (Haynes 1992; Darling and Wade 2008; Pawlowski and Holzmann 2008). It is therefore crucial to combine morphological analyses with molecular identification (also called DNA barcoding or genetic characterisation) to identify such cases (Hayward et al. 2004; Schweizer et al. 2005, 2009).

To combine molecular and morphological data for taxonomic purposes, a three-stage approach was proposed by Darling et al. (2016): *(i)* high resolution imaging of the test and molecular identification of the same individual, *(ii)* morphotype description produced only from the range of

test morphologies associated with the phylotype (see morphological description in Results) and *(iii)* allocation of the most appropriate taxonomic name by linking the phylotype-morphotype description to a taxonomic morphospecies description, using only strict morphological criteria. A further step to confirm the link between the phylotype and the taxonomic name would be to sequence topotypes, *i.e.* specimens coming from the type locality of the described species (Roberts et al. 2016). No formal comparison utilising the three-stage approach has yet been made for the nonionids.

Concerning the taxonomic identification of the five phylotypes presented in this study (Figure 2), T5 was previously identified as *Nonionellina labradorica* and T3 as *Nonionoides turgidus* in other studies (Table 2). Phylotype T2 was only identified at the generic level by Holzmann and Pawlowski (2017). Phylotype T4 specimens from Namibia (Grimm et al., *unpublished data*) and the Adriatic Sea (Holzmann and Pawlowski 2017) have only been identified morphologically at the generic level, whereas the T4 Californian specimen (Bernhard et al. 2006) was identified as *Nonionella stella* (Table 2). Because of the high sequence variability found in this phylotype, T4 may include different biological species. To address this issue, a better sampling effort with more individuals from each location is compulsory to investigate the potential inter-specific variation within this clade. In addition, more detailed analyses comparing molecular and morphological data using the three-stage approach (Darling et al. 2016) are still needed to confirm the taxonomic identification of phylotypes T2, T4 and T5.

When using only morphological criteria, the phylotype T1 closely resembles *Nonionella stella* with some specimens exhibiting digitated inner end of the last chamber. However, this morphological character is also shared by the Californian specimens identified in the Santa Barbara Basin (Bernhard et al. 2006), although the latter population is highly distinct genetically from the phylotype T1 (Figure 2). Our molecular results show clearly that the digitated inner end of the last chamber is not a robust morphological criterion alone to identify individuals at the species level, as different (and not closely related) nonionids (phylotypes T1 and T4) share this morphological characteristic. At this stage, there is no satisfactory taxonomic name available for the phylotype T1 and we propose to call it *Nonionella* sp. T1 for the time being. It sounds in fact too preliminary to call it *Nonionella stella* albeit there could be morphological evidence. Hence, sampling and sequencing live topotypes from the Cushman and Moyer reference site in San Pedro is the only way to characterise genetically and morphologically *N. stella*. This will allow determining whether the phylotype T1 does belong to *N. stella* or not. The same applies to the phylotype T4 found in the Santa Barbara Basin. As there is only one phylotype (T1) recognised presently in the Oslo- and the Gullmar fjords,

which exhibits a test with a more or less developed hand-shaped extension, the specimens previously found in these regions and identified morphologically as *N. stella* or *Nonionella* aff. *N. stella* are most likely *Nonionella* sp. T1.

When was Nonionella *sp. T1 introduced in the Oslofjord?*

Living (stained) individuals of *Nonionella* sp. T1 were first recorded in the inner Oslofjord in 2012 (Alve and Hess, *unpublished data*). In the Oslofjord core (this study), the first recorded *Nonionella* sp. T1 (one test only) was retrieved from the sediment layer dated around 1985, whereas no specimens were observed in the older layers (*i.e.* 8 to 12 cm) among the 2,250 identified foraminifers. These observations confirm that *Nonionella* sp. T1 was recently introduced in the Oslofjord. To more precisely define the date of introduction, the species was absent at station Cj3-2016 (inner Oslofjord) both in living and dead assemblages collected in 2009 (Hess, *unpublished live data*, Dolven et al. 2013). This suggests that *Nonionella* sp. T1 actually may not have been introduced in the Oslofjord in 1985. Species appearance in the sediment layer corresponding to 1985 can be explained by a number of causes such as mixing by bioturbation, deep infaunal microhabitat in the sediment or by an usuccessful first introduction (McGann et al. 2012). However, it seems that the species became acclimated in the area between 2009 and 2012. In our samples, all specimens observed down to 5 cm (corresponding to 2001) displayed a greenish coloration suggesting that they were alive or recently dead at the time of sampling. Indeed, benthic foraminifera may move actively on and in the sedimentary column (Severin and Erskian 1981; Gross 2002; Seuront and Bouchet 2015) and bioturbation by macrofaunal organisms (see above) may also cause downward transport of foraminifera to subsurface sediment layers (Langer et al. 1989; Bouchet et al. 2009). All these factors could explain the presence of *Nonionella* sp. T1 in layers older than 2012. The taxon's abundances are still quite low, about 5% in 2012 and down to only 1.5% in 2016 at the time of sampling. Hence, it is not yet possible to confirm that the species is established in the Oslofjord and further monitoring is required.

From where and how was Nonionella *sp. T1 introduced into the Oslofjord?*

Before appearing in the inner Oslofjord, *Nonionella* sp. T1 was introduced further south into the Skagerrak and the Gullmar fjord in 1985 (Polovodova Asteman and Schönfeld 2015). Since the population from Gullmar fjord settled prior to the one in the Oslofjord (Polovodova Asteman and Schönfeld 2015), *Nonionella* sp T1 observed in the latter may well have been transported from the Skagerrak.

Non-anthropogenic mediated transport from neighbouring areas, which is well studied in terrestrial invasion, can also contribute to the

introduction of foraminiferal NIS in new ecosystems *via* marine currents. Benthic foraminiferal propagules can be widely distributed by waves and currents (Alve and Goldstein 2003, 2010). Particularly, Ross and Hallock (2016) proposed that cosmopolitan species produce propagules with great potential for dispersal, while endemic taxa may have lost this basic characteristic. Current patterns in the adjacent Skagerrak area are dominated by the northward Baltic Current, which flows from the Kattegat – along the Swedish west coast (where Gullmar and Sannäs fjords are located) towards the entrance of the outer Oslofjord. At the Oslofjord entrance, the Baltic Current turns west and continues along the southern coast of Norway as the Norwegian Coastal Current (Figure 1). *Nonionella* sp. T1 has been recorded further south in the Øresund strait, Kattegat, the Skagerrak-Kattegat front and the Gullmar fjord (Polovodova Asteman and Schönfeld 2015; Charrieau et al. 2018) (Figure 5).

In order to confirm this hypothesis, we re-examined samples from the core IH60, which were collected in the Indre Hvaler Basin (Figure 1) on the Norwegian coast near the outer Oslofjord in 2008 (Bouchet and Alve, *unpublished data*). There was no *Nonionella* sp. T1 specimen found in the core, suggesting that the species was not yet present in the outer Oslofjord in 2008. To investigate this further, we re-examined two sediment cores (SSK09-4.5A and SSK10-4.5) for *Nonionella* sp. T1, which were taken in the deepest basin of the Swedish Sannäs fjord (Robijn 2012; Nordberg et al. 2017). The fjord is located between the Indre Hvaler and the Gullmar fjord (Figures 1, 5) and its dated sediment cores (see Robijn 2012; Nordberg et al. 2017 for more details) can thus provide information about northward transport of *Nonionella* sp. T1 propagules. Indeed, both cores demonstrate that *Nonionella* sp. T1 arrived in the area sometime between 1995 and 2009, but was found in consistently low relative abundances (always < 1% in the > 63 µm fraction) (*unpublished data*). Taking into account the potential bioturbation effect, the timing of *Nonionella* sp. T1 introduction in these areas is closer than those in the Oslofjord and supports the hypothesis of migration from the south.

Furthermore, in the Oslofjord, twenty-three marine invertebrate species have been introduced since the 1800s and some of them, such as the comb jelly *Mnemiopsis leydyi* (Faasse and Bayha 2006) and the diatom *Coscinodiscus wailesii* (Edwards et al. 2001) were transported in ballast water tanks. Hence, *Nonionella* sp. T1 may also have been introduced into the Oslofjord by ballast water of cargo ships, which has considerably increased since the 1870s. Ballast water tanks often contain estuarine and marine sediments, which are thought to be a powerful mean of benthic species dispersion across the world (Blanchard et al. 2002). Taken the fact that benthic foraminiferal propagules can survive for two years before growth commences (Alve and Goldstein 2010), they may significantly increase their survival rates in ballast water and sediment compared to other taxa.

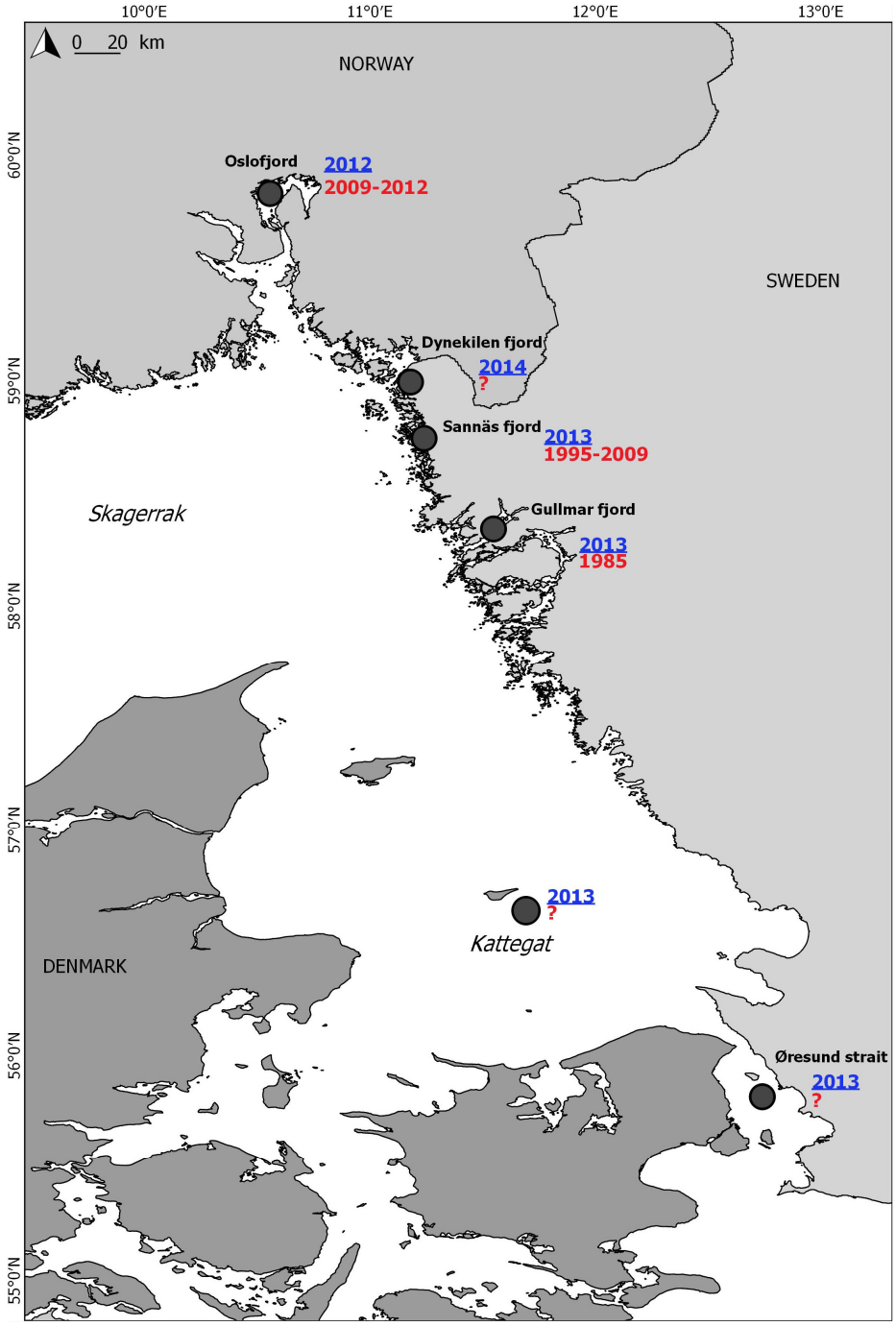

Figure 5. *Nonionella* sp. T1 records in Skagerrak-Kattegat and its adjacent fjords. Blue underlined dates correspond to the first observation time / Red dates correspond to the estimated introduction time. For details see Table S1.

Such behaviours could hence explain the presence of living foraminifera in ballast tanks (Galil and Hülsmann 1997).

An introduction pathway of *Nonionella* sp. T1 into the Oslofjord may be explained by propagule transport over short distances by currents from the south or by ballast water. For the moment, there are not enough molecular data available to trace the origin of *Nonionella* sp. T1 in the Skagerrak region. A worldwide sampling effort is needed to investigate the origin of this phylotype.

Can Nonionella *sp. T1 become an invasive species?*

Nonionella sp. T1 is a recent NIS in the Oslo-, Gullmar and Sannäs fjords benthic communities and is still present in low abundances (~ 5% in > 125 µm fraction, ~ 5% and < 1% in > 63 µm fraction, respectively) as compared to its populations in the Skagerrak (> 46%, > 63 µm fraction) and Dynekilen fjord (11%, > 63 µm fraction) (Polovodova Asteman and Schönfeld 2015). This is a classic feature of NIS that tends to have a short period of low abundances before it starts to increase when the species gets definitively established (McGann et al. 2012). Consequently, its status as an invasive species is yet to be investigated. The likelihood of an introduced species becoming invasive requires an understanding of its ecological requirements and role in the ecosystem functioning (Langer and Mouanga 2016). Unfortunately, although benthic foraminifera are present in high densities in the sediment, their role in the benthic ecosystem is still poorly studied (Murray 2006). Specifically, there is a limited knowledge about their trophic status and their impact on the particulate and dissolved fluxes *e.g.* nitrate, nitrite at the sediment water-interface whereas it is now known that foraminifera are involved in calcification, bioturbation and denitrifications processes (Gross 2002; Murray 2006; Piña-Ochoa et al. 2010; Seuront and Bouchet 2015).

Related morphospecies described under the name *N. stella* have been identified living in very different environmental conditions *e.g.* depth, temperature, salinity and oxygen concentration (Kitazato 1994; Bernhard et al. 1997; Maas 2000; Leiter and Altenbach 2010; Glock et al. 2013). Hence, a re-evaluation of these publications is required, as they most likely represent different species with different ecological requirements. The *Nonionella* morphospecies from the Santa Barbara Basin, California, described morphologically as *Nonionella stella*, is able to sequester chloroplasts from diatoms (Grzymski et al. 2002) and may switch to denitrification in the absence of oxygen (Risgaard-Petersen et al. 2006). This strategy confers an advantage to this species to survive in anoxic conditions (Bernhard et al. 2012). Such survival strategy, together with its prolific reproduction and rapid maturation (Silva et al. 1996), could explain the morphospecies dominance in numerous ecosystems *e.g.* anoxic basins off California (Bernhard and Bowser 1999), oxygen minimum zones (Glock et al. 2013) and deep sea environments (Silva et al. 1996). Furthermore, in the Gullmar fjord, *Nonionella* sp. T1 highest abundances have followed episodes of severe hypoxia in winters between 1987 and 1995 (Filipsson and Nordberg 2004). Increasing abundances of *Nonionella* sp. T1 since its introduction into the Gullmar fjord in 1985 suggest that the species would benefit, similarly to *Stainforthia fusiformis* introduced earlier in the 1970s, from the oxygen-depleted conditions.

Stainforthia fusiformis is an opportunistic species known to dominate fjords in the Skagerrak with severe oxygen depletion (Alve 2003) and

degraded ecological quality statuses (Dolven et al. 2013). At station Cj3-2016, inner Oslofjord, *Nonionella* sp. T1 co-occurs with the following morphospecies: *Adercotryma wrighti, Reophax subfusiformis, Bulimina marginata, Nonionellina labradorica* and *Stainforthia fusiformis*. From 1996 to 2016, the abundance of *S. fusiformis* increased from 10 to 50% while the abundance of *B. marginata* decreased from 40 to 16% of the assemblage in the > 125 µm fraction. The co-occurrence of *S. fusiformis* with *Nonionella* sp. T1 suggests that the latter can be an opportunistic species as well. Hence, *Nonionella* morphospecies may be opportunistic and plastic species able to adapt to changing environmental conditions from oxic to anoxic. The species' adaptability would give it an advantage in becoming invasive in the Oslofjord. At this stage, it is not yet possible to suggest any trophic competition with *Nonionoides turgidus* and *Nonionellina labradoric*a for instance, which are the indigenous morphological counterparts of *Nonionella* sp. T1. Hence, further studies are needed to evaluate temporal population dynamics, the role of *Nonionella* sp. T1 in the functioning of the benthic ecosystems and the effect of this species on the foraminiferal assemblages.

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References

Almogi-Labin A, Hyams-Kaphzan O (2012) *Epistomaroides punctatus* (Said, 1949) - a new alien foraminifera found at Akhziv - Rosh Hanikra, northern Israel, eastern Mediterranean Sea. *Mediterranean Marine Science* 13: 294–296, https://doi.org/10.12681/mms.311

Alve E (2003) A common opportunistic foraminiferal species as an indicator of rapidly changing conditions in a range of environments. *Estuarine, Coastal and Shelf Science* 57: 501–514, https://doi.org/10.1016/S0272-7714(02)00383-9

Alve E, Goldstein ST (2003) Propagule transport as a key method of dispersal in benthic foraminifera (Protista). *Limnology and Oceanography* 48: 2163–2170, https://doi.org/10.4319/lo.2003.48.6.2163

Alve E, Goldstein ST (2010) Dispersal, survival and delayed growth of benthic foraminiferal propagules. *Journal of Sea Research* 63: 36–51, https://doi.org/10.1016/j.seares.2009.09.003

Alve E, Nagy J (1990) Main feature of foraminiferal distribution reflecting estuarine hydrography in Oslofjord. *Marine Micropaleontology* 16: 181–206, https://doi.org/10.1016/0377-8398(90)90003-5

Alve E, Lepland A, Magnusson J, Backer-Owe K (2009) Monitoring strategies for re-establishment of ecological reference conditions: possibilities and limitations. *Marine Pollution Bulletin* 59: 297–310, https://doi.org/10.1016/j.marpolbul.2009.08.011

Anisimova M, Gascuel O (2006) Approximate likelihood-ratio test for branches: a fast, accurate and powerful alternative. *Systematic Biology* 55: 539–552, https://doi.org/10.1080/10635150600755453

Appleby PG (2001) Chronostratigraphic techniques in recent sediments. In: Last WM, Smol JP (eds), Tracking Environmental Change Using Lake Sediments Volume 1: Basin Analysis, Coring, and Chronological Techniques. Kluwer Academic Publishers, The Netherlands, pp 117–203

Asano K (1936) *Pseudononion*, a new genus of foraminifera found in Muraoka-mura, Kamakura-gôri, Kanagawa prefecture. *The Journal of the Geological Society of Japan* 43: 347–348, https://doi.org/10.1248/cpb.37.3229

Bax N, Williamson A, Aguero M, Gonzalez E, Geeves W (2003) Marine invasive alien species: a threat to global biodiversity. *Marine Policy* 27: 313–323, https://doi.org/10.1016/S0308-597X(03)00041-1

Bernhard JM, Bowser SS (1999) Benthic foraminifera of dysoxic sediments: chloroplast sequestering and functional morphology. *Earth-Science Reviews* 46: 149–165, https://doi.org/10.1016/S0012-8252(99)00017-3

Bernhard JM, Sen Gupta BK, Borne PF (1997) Benthic foraminiferal proxy to estimate dysoxic bottom-water oxygen concentrations: Santa Barbara basin, US Pacific continental margin. *Journal of Foraminiferal Research* 27: 301–310, https://doi.org/10.2113/gsjfr.27.4.301

Bernhard JM, Habura A, Bowser SS (2006) An endobiont-bearing allogromiid from the Santa Barbara Basin: implications for the early diversification of foraminifera. *Journal of Geophysical Research* 111: G3002, https://doi.org/10.1029/2005JG000158

Bernhard JM, Casciotti KL, McIlvin MR, Beaudoin DJ, Visscher PT, Edgcomb VP (2012) Potential importance of physiologically diverse benthic foraminifera in sedimentary nitrate storage and respiration. *Journal of Geophysical Research* 117: 1–14, https://doi.org/10.1029/2012JG001949

Blanchard AL, Feder HM, Shaw DG (2002) Long-term investigation of benthic fauna and the influence of treated ballast water disposal in Port Valdez, Alaska. *Marine Pollution Bulletin* 44: 367–382, https://doi.org/10.1016/S0025-326X(01)00246-6

Bouchet VMP, Debenay JP, Sauriau PG (2007) First report of *Quinqueloculina carinatastriata* (Wiesner, 1923) (Foraminifera) along the french Atlantic coast (Marennes-Oleron Bay and Ile De Re). *Journal of Foraminiferal Research* 37: 204–212, https://doi.org/10.2113/gsjfr.37.3.204

Bouchet VMP, Sauriau PG, Debenay JP, Mermillod-Blondin F, Schmidt S, Amiard JC, Dupas B (2009) Influence of the mode of macrofauna-mediated bioturbation on the vertical distribution of living benthic foraminifera: first insight from axial tomodensitometry. *Journal of Experimental Marine Biology and Ecology* 371: 20–33, https://doi.org/10.1016/j.jembe.2008.12.012

Butchart SHM, Walpole M, Collen B, Strien A van, Scharlemann JPW, Almond REA, Baillie JEM, Bomhard B, Brown C, Bruno J, Carpenter KE, Carr GM, Chanson J, Chenery AM, Csirke J, Davidson NC, Dentener F, Foster M, Galli A, Galloway JN, Genovesi P, Gregory RD, Hockings M, Kapos V, Lamarque JF, Leverington F, Loh J, McGeoch MA, McRae L, Minasyan A, Morcillo MH, Oldfield TEE, Pauly D, Quader S, Revenga C, Sauer JR, Skolnik B, Spear D, Stanwell-Smith D, Stuart SN, Symes A, Tierney M, Tyrrell TD, Vie JC, Watson R (2010) Global biodiversity: indicators of recent declines. *Science* 328: 1164–1168, https://doi.org/10.1126/science.1187512

Calvo-Marcilese L, Langer MR (2010) Breaching biogeographic barriers: the invasion of *Haynesina germanica* (Foraminifera, Protista) in the Bahía Blanca estuary, Argentina. *Biological Invasions* 12: 3299–3306, https://doi.org/10.1007/s10530-010-9723-x

Carlton JT (1987) Patterns of transoceanic marine biological invasions in the Pacific-Ocean. *Bulletin of Marine Science* 41(2): 452–465

Carlton JT, Geller JB (1993) Ecological roulette: the global transport of nonindigenous marine organisms. *Science* 261: 78–82, https://doi.org/10.1126/science.261.5117.78

Charrieau LM, Filipsson HL, Ljung K, Chierici M, Knudsen KL, Kritzberg E (2018) The effects of multiple stressors on the distribution of coastal benthic foraminifera: a case study from the Skagerrak-Baltic Sea region. *Marine Micropaleontology* 139: 42–56, https://doi.org/10.1016/j.marmicro.2017.11.004

Culver SJ, Buzas MA (1987) Distribution of recent benthic foraminifera off the Pacific coast of Mexico and Central America. *Smithsonian Contributions to the Marine Sciences* 30: 1–84, https://doi.org/10.5479/si.01960768.30.1

Cushman JA (1926) Recent foraminifera from Porto Rico. *Cushman Laboratory for Foraminiferal Research Contributions* 2: 53–76

Cushman JA, Moyer DA (1930) Some recent foraminifera from off San Pedro, California. *Cushman Laboratory for Foraminiferal Research Contributions* 6: 49–62

Cushman, JA (1939) A monograph of the foraminiferal family Nonionidae. *USGS Series Professional Paper* 191: 100 pp, https://doi.org/10.3133/pp191

Darling KF, Wade CM (2008) The genetic diversity of planktic foraminifera and the global distribution of ribosomal RNA genotypes. *Marine Micropaleontology* 67: 216–238, https://doi.org/10.1016/j.marmicro.2008.01.009

Darling KF, Schweizer M, Knudsen KL, Evans KM, Bird C, Roberts A, Filipsson HL, Kim JH, Gudmundsson G, Wade CM, Sayer MDJ, Austin WEN (2016) The genetic diversity, phylogeography and morphology of Elphidiidae (Foraminifera) in the north-east Atlantic. *Marine Micropaleontology* 129: 1–23, https://doi.org/10.1016/j.marmicro.2016.09.001

Dawson JW (1860) Notice of the tertiary fossils from Labrador, Maine, etc. and remarks on the climate of Canada in the newer Pliocene of Pleistocene period. *Canadian Naturalist* 5: 188–200

Dolven JKL, Elisabeth A, Brage R, Jan M (2013) Defining past ecological status and in situ reference conditions using benthic foraminifera: a case study from the Oslofjord, Norway. *Ecological Indicators* 29: 219–233, https://doi.org/10.1016/j.ecolind.2012.12.031

Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797, https://doi.org/10.1093/nar/gkh340

Edwards M, John AWG, Johns DG, Reid PC (2001) Case history and persistence of the non-indigenous diatom *Coscinodiscus wailesii* in the north-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 81: 207–211, https://doi.org/10.1017/S0025315401003654

Faasse MA, Bayha KM (2006) The ctenophore *Mnemiopsis leidyi* A. Agassiz 1865 in coastal water of the Netherlands: an unrecognized invasion? *Aquatic Invasions* 1: 270–277, https://doi.org/10.3391/ai.2006.1.4.10

Filipsson HL, Nordberg K (2004) A 200-year environmental record of a low-oxygen fjord, Sweden, elucidated by benthic foraminifera, sediment characteristics and hydrographic data. *Journal of Foraminiferal Research* 34: 277–293, https://doi.org/10.2113/34.4.277

Galil B, Hülsmann N (1997) Protist transport via ballast water—biological classification of ballast tanks by food web interactions. *European Journal of Protistology* 33: 244–253, https://doi.org/10.1016/S0932-4739(97)80002-8

Gascuel O (1997) BIONJ: an improved version of the NJ algorithm based on a simple model of sequence data. *Molecular Biology and Evolution* 14: 685–695, https://doi.org/10.1093/oxfordjournals.molbev.a025808

Glock N, Schönfeld J, Eisenhauer A, Hensen C, Mallon J, Sommer S (2013) The role of benthic foraminifera in the benthic nitrogen cycle of the Peruvian oxygen minimum zone. *Biogeosciences* 10: 4767–4783, https://doi.org/10.5194/bg-10-4767-2013

Gollasch S, Haydar D, Minchin D, Wolff WJ, Reise K (2009) Introduced aquatic species of the North Sea coasts and adjacent brackish waters. In: Rilov G, Crooks JA (eds), Biological Invasions in Marine Ecosystems. Springer-Verlag Berlin Heidelberg, pp 507–528, https://doi.org/10.1007/978-3-540-79236-9_29

Gouy M, Guindon S, Gascuel O (2010) Sea view version 4: a multiplatform graphical user interface for sequence alignment and phylogenetic tree building. *Molecular Biology and Evolution* 27: 221–224, https://doi.org/10.1093/molbev/msp259

Grenfell HR, Hayward BW, Horrocks M (2007) Foraminiferal record of ecological impact of deforestation and oyster farms, Mahurangi Harbour, New Zealand. *Marine and Freshwater Research* 58: 475–491, https://doi.org/10.1071/MF06155

Gross O (2002) Sediment interactions of foraminifera: implications for food degradation and bioturbation processes. *Journal of Foraminiferal Research* 32: 414–424, https://doi.org/10.2113/0320414

Grzymski J, Schofield OM, Falkowski PG, Bernhard JM (2002) The function of plastids in the deep-sea benthic foraminifer, *Nonionella stella*. *Limnology and Oceanography* 47: 1569–1580, https://doi.org/10.4319/lo.2002.47.6.1569

Guindon S, Gascuel O (2003) A simple, fast, and accurate algorithm to estimate large phylogenies by Maximum Likelihood. *Systematic Biology* 52: 696–704, https://doi.org/10.1080/10635150390235520

Haynes JR (1992) Supposed pronounced ecophenotypy in foraminifera. *Journal of Micropalaeontology* 11: 59–63, https://doi.org/10.1144/jm.11.1.59

Hayward BW (1997) Introduced marine organisms in New Zealand and their impact in the Waitemata Harbour, Auckland. *Tane* 36: 197–223

Hayward BW, Grenfell HR, Reid CM, Hayward KA (1999) Recent New Zealand shallow-water benthic foraminifera: taxonomy, ecologic distribution, biogeography, and use in paleoenvironmental assessment. Institute of Geological and Nuclear Sciences Monograph 21, 258 pp

Hayward BW, Holzmann M, Grenfell HR, Pawlowski J, Triggs CM (2004) Morphological distinction of molecular types in Ammonia - towards a taxonomic revision of the world's most commonly misidentified foraminifera. *Marine Micropaleontology* 50: 237–271, https://doi.org/10.1016/S0377-8398(03)00074-4

Heron-Allen E, Earland A (1930) The foraminifera of the Plymouth district. *Journal of the Royal Microscopical Society* 50: 46–84, https://doi.org/10.1111/j.1365-2818.1930.tb01475.x

Heron-Allen E, Earland A (1932) Foraminifera: part 1, the ice free area of the Falkland Island and adjacent seas. *Discovery Reports University Press* 4: 291–460

Hess S, Alve E, Reuss N (2014) Benthic foraminiferal recovery in the Oslofjord (Norway): responses to capping and re-oxygenation. *Estuarine, Coastal and Shelf Science* 147: 87–102, https://doi.org/10.1016/j.ecss.2014.05.012

Holzmann M, Pawlowski J (2017) An updated classification of Rotaliid foraminifera based on ribosomal DNA phylogeny. *Marine Micropaleontology* 132: 18–34, https://doi.org/10.1016/j.marmicro.2017.04.002

Hyams-Kaphzan O, Almogi-Labin A, Sivan D, Benjamini C (2008) Benthic foraminifera assemblage change along the southeastern Mediterranean inner shelf due to fall-off of Nile-derived siliciclastics. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen* 248: 315–344, https://doi.org/10.1127/0077-7749/2008/0248-0315

Ingle J, Keller G, Kolpack RL (1980) Benthic foraminiferal biofacies, sediments and water masses of the Southern Peru-Chile Trench Area, Southeastern Pacific Ocean. *Micropaleontology* 26: 113–150, https://doi.org/10.2307/1485435

Kato M (1992) Benthic foraminifers from the Japan Sea: leg 11. In: Proceedings of the Ocean Drilling Program, Scientific Results 127/128. Ocean Drilling Program, College Station, TX, pp 365–392

Kimura M (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* 16: 111–120, https://doi.org/10.1007/BF01731581

Kitazato H (1994) Foraminiferal microhabitats in four marine environments around Japan. *Marine Micropaleontology* 24: 29–41, https://doi.org/10.1016/0377-8398(94)90009-4

Kite-Powell HL (2008) Shipping and ports. Encyclopedia of Ocean Sciences: Second Edition 5: 2768–2776, https://doi.org/10.1016/B978-012374473-9.00495-1

Langer M, Hottinger L, Huber B (1989) Functional morphology in low-diverse benthic foraminiferal assemblages from tidal flats of the North Sea. *Senckenbergiana Maritima-Series* 20: 81−99

Langer MR (2008) Assessing the contribution of foraminiferan protists to global ocean carbonate production. *Journal of Eukaryotic Microbiology* 55: 163–169, https://doi.org/10.1111/j.1550-7408.2008.00321.x

Langer MR, Mouanga GH (2016) Invasion of Amphisteginid foraminifera in the Adriatic Sea. *Biological Invasions* 18: 1335–1349, https://doi.org/10.1007/s10530-016-1070-0

Lankford RR, Phleger FB (1973) Foraminifera from the nearshore turbulent zone, western North America. *Journal of Foraminiferal Research* 3: 101–132, https://doi.org/10.2113/gsjfr.3.3.101

Leiter C, Altenbach AV (2010) Benthic foraminifera from the diatomaceous mud belt off Namibia: characteristic species for severe anoxia. *Palaeontologia Electronica* 13(2): 1–19

Maas M (2000) Verteilung lebendgefärbter bentischer Foraminiferen in einer intensivierten Sauerstoffminimumzone, Indo-Pakistanischer Kontinentalrand, nördliches Arabisches Meer. *Meyniana* 52: 101–129

Martins MVA, Helali MA, Zaaboub N, Boukef-BenOmrane I, Frontalini F, Reis D, Portela H, Clemente IMMM, Nogueira L, Pereira E, Miranda P, Bour M El, Aleya L (2016) Organic matter quantity and quality, metals availability and foraminiferal assemblages as environmental proxy applied to the Bizerte Lagoon (Tunisia). *Marine Pollution Bulletin* 105: 161–179, https://doi.org/10.1016/j.marpolbul.2016.02.032

McGann M, Sloan D (1996) Recent introduction of the foraminifer Trochammina hadai Uchio into San Francisco Bay, California, USA. *Marine Micropaleontology* 28: 1–3, https://doi.org/10.1016/0377-8398(95)00077-1

McGann M, Sloan D, Cohen AN (2000) Invasion by a Japanese marine microorganism in western North America. *Hydrobiologia* 421: 25–30, https://doi.org/10.1023/A:1003808517945

McGann M, Grossman EE, Takesue RK, Penttila D, Walsh JP, Corbett R (2012) Arrival and expansion of the invasive foraminifera *Trochammina hadai* Uchio in Padilla Bay, Washington. *Northwest Science* 86: 9–26, https://doi.org/10.3955/046.086.0102

Merkado G, Holzmann M, Apothéloz-Perret-Gentil L, Pawlowski J, Abdu U, Almogi-Labin A, Hyams-Kaphzan O, Bakhrat A, Abramovich S (2013) Molecular evidence for Lessepsian invasion of Soritids (larger symbiont bearing benthic foraminifera). *PLoS ONE* 8: e77725, https://doi.org/10.1371/journal.pone.0077725

Merkado G, Titelboim D, Hyams-Kaphzan O, Holzmann M, Pawlowski J, Almogi-Labin A, Abdu U, Herut B, Abramovich S (2015) Molecular phylogeny and ecology of Textularia agglutinans d'Orbigny from the Mediterranean coast of Israel: a case study of a successful new incumbent. PLoS ONE 10: e0142263, doi: 10.1371/journal.pone.0142263.g001, https://doi.org/10.1371/journal.pone.0142263.g001

Milker Y, Schmiedl G (2012) A taxonomic guide to modern benthic shelf foraminifera of the western Mediterranean Sea. *Palaeontologia Electronica* 15: 1–134, https://doi.org/10.26879/271

Murray JW (2006) Ecology and applications of benthic foraminifera. Cambridge University Press, Cambridge, 426 pp, https://doi.org/10.1017/CBO9780511535529

Niemistö L (1974) A gravity corer for studies of soft sediments. *Havforskningsinst Skr Helsinki* 238: 33–38

Nordberg K, Polovodova Asteman I, Gallagher TM, Robijn A (2017) Recent oxygen depletion and benthic faunal change in shallow areas of Sannäs Fjord, Swedish west coast. *Journal of Sea Research* 127: 46–62, https://doi.org/10.1016/j.seares.2017.02.006

Occhipinti-Ambrogi A, Marchini A, Cantone G, Castelli A, Chimenz C, Cormaci M, Froglia C, Furnari G, Gambi MC, Giaccone G, Giangrande A, Gravili C, Mastrototaro F, Mazziotti C,

Orsi-Relini L, Piraino S (2010) Alien species along the Italian coasts: an overview. *Biological Invasions* 13: 215–237, https://doi.org/10.1007/s10530-010-9803-y

Oflaz SA (2006) Taxonomy and distribution of the benthic foraminifera in the Gulf of Iskenderun, eastern Mediterranean. PhD Thesis, Middle East Technical University, Ankara, Turkey, 306 pp

Oliveira OMP (2007) The presence of the ctenophore *Mnemiopsis leidyi* in the Oslofjorden and considerations on the initial invasion pathways to the North and Baltic Seas. *Aquatic Invasions* 2: 185–189, https://doi.org/10.3391/ai.2007.2.3.5

Patterson RT, Guilbault JP, Thomson RE (2000) Oxygen level control on foraminiferal distribution in Effingham Inlet, Vancouver Island, British Columbia, Canada. *Journal of Foraminiferal Research* 30: 321–335, https://doi.org/10.2113/0300321

Pawlowski J (2000) Introduction to the molecular systematics of foraminifera. *Micropaleontology* 46: 1–12

Pawlowski J, Holzmann M (2008) Diversity and geographic distribution of benthic foraminifera: a molecular perspective. *Biodiversity and Conservation* 17: 317–328, https://doi.org/10.1007/s10531-007-9253-8

Pawlowski J, Holzmann M (2014) A plea for DNA barcoding of foraminifera. *Journal of Foraminiferal Research* 44: 62–67, https://doi.org/10.2113/gsjfr.44.1.62

Piña-Ochoa E, Koho KA, Geslin E, Risgaard-Petersen N (2010) Survival and life strategy of the foraminiferan *Globobulimina turgida* through nitrate storage and denitrification. *Marine Ecology Progress Series* 417: 39–49, https://doi.org/10.3354/meps08805

Polovodova Asteman I, Schönfeld J (2015) Recent invasion of the foraminifer *Nonionella stella* Cushman & Moyer, 1930 in northern European waters: evidence from the Skagerrak and its fjords. *Journal of Micropalaeontology* 35: 20–25, https://doi.org/10.1144/jmpaleo2015-007

Pyšek P, Richardson DM (2010) Invasive species, environmental change and management, and health. *Annual Review of Environment and Resources* 35: 25–55, https://doi.org/10.1146/annurev-environ-033009-095548

Risgaard-Petersen N, Langezaal AM, Ingvardsen S, Schmid MC, Jetten MSM, Op den Camp HJM, Derksen JWM, Piña-Ochoa E, Eriksson SP, Peter Nielsen L, Peter Revsbech N, Cedhagen T, Zwaan GJ van der (2006) Evidence for complete denitrification in a benthic foraminifer. *Nature* 443: 93–96, https://doi.org/10.1038/nature05070

Roberts A, Austin W, Evans K, Bird C, Schweizer M, Darling K (2016) A new integrated approach to taxonomy: the fusion of molecular and morphological systematics with type material in benthic foraminifera. *PLoS ONE* 11: e0158754, https://doi.org/10.1371/journal.pone.0158754

Robijn A (2012) A 250 years sediment record from the Sannäsfjord, Swedish west coast, environmental changes reflected by benthic foraminifera and heavy metal concentrations. Master Thesis, Department of Earth Sciences, University of Gothenburg, 27 pp

Ross BJ, Hallock P (2016) Dormancy in the Foraminifera: a review. *Journal of Foraminiferal Research* 46: 358–368, https://doi.org/10.2113/gsjfr.46.4.358

Rhumbler L (1949) Special Note: plate explanation of Rhumbler's "Plankton-Expedition". *The Micropaleontologist* 3: 33–40, https://doi.org/10.2307/1484023

Sakai AK, Allendorf FW, Holt JS, Lodge M, Molofsky J, With KA, Cabin RJ, Cohen JE, Norman C, Mccauley DE, Neil PO, Parker M, Thompson JN, Weller SG (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics* 32: 305–332, https://doi.org/10.1146/annurev.ecolsys.32.081501.114037

Schweizer M (2006) Evolution and molecular phylogeny of *Cibicides* and *Uvigerina* (Rotaliida, Foraminifera). *Geologica Ultraiectina* 261: 1–167

Schweizer M, Pawlowski J, Duijnstee IAP, Kouwenhoven TJ, Zwaan GJ Van Der (2005) Molecular phylogeny of the foraminiferal genus *Uvigerina* based on ribosomal DNA sequences. *Marine Micropaleontology* 57: 51–67, https://doi.org/10.1016/j.marmicro.2005.07.001

Schweizer M, Pawlowski J, Kouwenhoven T, Zwaan B van der (2009) Molecular phylogeny of common Cibicidids and related Rotaliida (Foraminifera) based on small subunit rDNA sequences. *Journal of Foraminiferal Research* 39: 300–315, https://doi.org/10.2113/gsjfr.39.4.300

Schweizer M, Polovodova I, Nikulina A, Schönfeld J (2011) Molecular identification of *Ammonia* and *Elphidium* species (Foraminifera, Rotaliida) from the Kiel Fjord (SW Baltic Sea) with rDNA sequences. *Helgoland Marine Research* 65: 1–10, https://doi.org/10.1007/s10152-010-0194-3

Seebens H, Schwartz N, Schupp PJ, Blasius B (2016) Predicting the spread of marine species introduced by global shipping. *Proceedings of the National Academy of Sciences* 113: 5646–5651, https://doi.org/10.1073/pnas.1524427113

Seuront L, Bouchet VMP (2015) The devil lies in details: new insights into the behavioural ecology of intertidal Foraminifera. *Journal of Foraminiferal Research* 45: 390–401, https://doi.org/10.2113/gsjfr.45.4.390

Severin KP, Erskian MG (1981) Laboratory experiments on the vertical movement of *Quinqueloculina impressa* Reuss through sand. *Journal of Foraminiferal Research* 11: 133–136, https://doi.org/10.2113/gsjfr.11.2.133

Silva KA, Corliss BH, Rathburn AE, Thunell RC (1996) Seasonality of living benthic foraminifera from the San Pedro Basin, California borderland. *Journal of Foraminiferal Research* 26: 71–93, https://doi.org/10.2113/gsjfr.26.1.71

Tapiero I (2002) No high-resolution paleoecologic and paleoclimatic changes of the Holocene, based on benthic foraminifera and sediments from the Mediterranean inner shelf, Israel. Beer Sheva, Israel, 130 pp

Tavaré S (1986) Some probabilistic and statistical problems in the analysis of DNA sequences. *American Mathematical Society* 17: 57–86

Uchio T (1962) Influence of the River Sidnano on foraminifera and sediment grain size distributions. *Publication of the Seto Marine Laboratory, Kyoto University, Sirahama, Japan* 10: 363–392, https://doi.org/10.5134/175306

Voisin M, Engel CR, Viard F (2005) Differential shuffling of native genetic diversity across introduced regions in a brown alga: aquaculture vs. maritime traffic effects. *Proceedings of the National Academy of Sciences* 102: 5432–5437, https://doi.org/10.1073/pnas.0501754102

Weber AAT, Pawlowski J (2014) Wide occurrence of SSU rDNA intragenomic polymorphism in foraminifera and its implication for molecular species identification. *Protist* 165: 645–661, https://doi.org/10.1016/j.protis.2014.07.006

Williamson WC (1858) On the recent foraminifera of Great Britain. Ray Society, London, 107 pp, https://doi.org/10.5962/bhl.title.139719

Wonham MJ, Carlton JT, Ruiz GM, Smith LD (2000) Fish and ships: relating dispersal frequency to success in biological invasions. *Marine Biology* 136: 1111–1121, https://doi.org/10.1007/s002270000303

Zenetos A, Gofas S, Verlaque M, Çinar ME, Garcia Raso JE, Bianchi CN, Morri C, Azzurro E, Bilecenoglu M, Froglia C, Siokou I, Violanti D, Sfriso A, San Martin G, Giangrande A, Mastrototaro F, Katağan T, Ballesteros E, Ramos-Espla A, Mastrototaro F, Ocana O, Zingone A, Gambi MC, Streftaris N (2010) Alien species in the Mediterranean Sea by 2010. A contribution to the application of European Union's Marine Strategy Framework Directive (MSFD). Part I. Spatial distribution. *Mediteranean Marine Science* 11: 381–493, https://doi.org/10.12681/mms.87

Zenetos A, Gofas S, Morri C, Rosso A, Violanti D, García Raso JE, Çinar ME, Almogi Labin A, Ates A, Azzuro E, Ballesteros E, Bianchi CN, Bilecenoglu M, C GM, Giangrande A, Gravili C, Hyams-Kaphzan O, Karachle V, Katsanevakis S, Lipej L, Mastrototaro F, Mineur F, Pancucci-Papadopoulou MA, Ramos Esplá A, Salas C, San Martín G, Sfriso A, Streftaris N, Verlaque M (2012) Alien species in the Mediterranean Sea by 2012. A contribution to the application of European Union's Marine Strategy Framework Directive (MSFD). Part 2. Introduction trends and pathways. *Mediteranean Marine Science* 13: 328–352, https://doi.org/10.12681/mms.327

Supplementary material

The following supplementary material is available for this article:

Table S1. Geo-referenced records of *Nonionella* sp. T1 in Skagerrak-Kattegat and its adjacent fjords.
Figure S1. Scanning Electronic Microscope (SEM) images of *Nonionella* sp. T1 unsequenced from the Gullmarfjord.
Figure S2. Scanning Electronic Microscope (SEM) images of *Nonionella* sp. T1 sequenced from the Gullmarfjord.
Figure S3. Scanning Electronic Microscope (SEM) images of *Nonionella* sp. T1 sequenced from the Oslofjord.
Figure S4. Scanning Electronic Microscope (SEM) images of *Nonionella* sp. T1 unsequenced from the Oslofjord.
Figure S5. Dry bulk density ($g.cm^{-3}$), ^{210}Pb and ^{137}Cs profiles of Cj3 core (Oslofjord).

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